Decline in Pelagic Cephalopod Metabolism With Habitat Depth Reflects Differences in Locomotory Efficiency

BRAD A. SEIBEL, ERIK V. THUESEN[1], JAMES J. CHILDRESS, AND LAURA A. GORODEZKY[2]

Oceanic Biology Group, Marine Science Institute, University of California, Santa Barbara, California 93106

Abstract. The metabolic rates of 33 species of pelagic cephalopods from California and Hawaii were measured and correlated with minimum depth of occurrence. Mean metabolic rates ranged from 0.07 μmol O_2 g^{-1} h^{-1} for the deep-living vampire squid, *Vampyroteuthis infernalis*, to 8.79 μmol O_2 g^{-1} h^{-1} for *Gonatus onyx*, a vertically migrating squid. An individual of *V. infernalis*, which lives within the oxygen minimum layer off California, had the lowest mass-specific metabolic rate ever measured for a cephalopod (0.02 μmol O_2 g^{-1} h^{-1}, 1050 g wet weight). For species collected in sufficient quantity and size range, metabolism was related to body size. Critical partial pressures of oxygen (P_c) were determined for Hawaiian and Californian cephalopods. P_c values for Hawaiian animals were considerably higher than for those taken off California, a trend that corresponds to the higher levels of environmental oxygen in the Hawaiian waters. Buffering capacity (β) of mantle muscle, assayed in eight cephalopod species, was used to estimate the capacity for glycolytic energy production. Mean β ranged from 1.43 slykes for a bathypelagic octopod, *Japetella heathi*, to 77.08 slykes for an epipelagic squid, *Sthenoteuthis oualaniensis*. Significant declines with increasing depth of occurrence were observed for both metabolism and β. The decline in metabolic parameters with depth is interpreted as a decreased reliance on locomotory abilities for predator/prey interactions in the light-limited deep sea. The decline in metabolism with depth observed for pelagic cephalopods was significantly steeper than that previously observed for either pelagic fishes or crustaceans. We suggest that since strong locomotory abilities are not a priority in the deep sea, deeper-living cephalopods may rely more heavily on means of locomotion that are more efficient than jet propulsion *via* mantle contractions—means such as fin swimming or medusoid swimming utilizing the arms and extensive webbing present in many deep-living species. The greater efficiency of deeper-living cephalopods may be responsible for the observation that the decline in metabolic rates with depth is more pronounced for pelagic cephalopods than for fishes or crustaceans.

Introduction

Cephalopods are morphologically diverse, visually orienting predatory molluscs. The five groups of extant cephalopods—squids (Teuthoidea), cuttlefishes (Sepioidea), octopuses (Octopoda), vampire squids (Vampyromorpha), and the chambered Nautilus (Nautiloidea)—are easily distinguished by morphological characteristics, among which are locomotory adaptations to their habitat (Roper *et al.*, 1984). Locomotory differences are also reflected in an animal's physiological properties. Previous physiological studies on cephalopods have primarily focused on the more commercially important squids, and on the shallow-water octopuses and cuttlefishes (Grieshaber and Gäde, 1976; Baldwin, 1982; O'Dor, 1982; O'Dor and Webber, 1986; Portner *et al.*, 1993).

Some of these animals are among the most metabolically active poikilotherms known (O'Dor and Shadwick, 1989), which stems in part from the inherent inefficiency of jet propulsion. Other studies have investigated the metabolism of *Nautilus* spp. and its ability to withstand low levels of oxygen (O'Dor *et al.*, 1990; Wells *et al.*, 1992; Boutilier *et al.*, 1996). Very little is known, however, about the physiological adaptations of cephalopods to the deep sea. The current study is a comprehensive comparison of the metabolic rates of midwater cephalopods living at depths down to 2 km off California and Hawaii.

Many studies have demonstrated a decline in the metabolic rates of pelagic fishes and crustaceans with increasing habitat depth (Childress, 1975; 1995; Torres *et al.*, 1979; Torres and Somero, 1988; Ikeda, 1988; Cowles *et al.*, 1991). Additional studies found no clear relationship between metabolism and minimum depth of occurrence in chaetognaths and medusae (Thuesen and Childress, 1993a, 1994). Bathypelagic representatives of these groups have metabolic rates comparable to those of their epipelagic counterparts when measured at the same temperature.

Childress and Mickel (1985) put forth the visual interactions hypothesis to explain the decline in metabolic rates of fish and crustaceans with increasing minimum depth of occurrence. They observed that reduced metabolic rates reflect decreased locomotory abilities in many deeper-living groups. They hypothesized that this decrease resulted from relaxed selection for strong locomotory abilities for visually cued predator/prey interactions in the low ambient light levels of the deep sea. Although deep-living fishes and crustaceans do possess well-developed eyes, these are apparently used primarily for interactions *via* bioluminescence (Marshall, 1979), which is a relatively weak, often transient light source. Under these conditions, interactions are likely to take place over short distances that do not require strong locomotory abilities (Marshall, 1979; Herring *et al.*, 1994; Fleisher and Case, 1995). The visual interactions hypothesis is supported by the presence of a decline in metabolic rates of visually orienting pelagic groups (fishes and crustaceans), and by the absence of a decline in non-visually orienting gelatinous organisms (*e.g.*, chaetognaths and medusae).

Cephalopods, like fishes and crustaceans, are highly visual predators that occupy a range of depths and habitats. As such, they are an obvious choice for further testing of the visual interactions hypothesis. In the present study, the oxygen consumption rates of 33 species of pelagic cephalopods were measured and correlated with minimum depth of occurrence. Because of differences in local productivity and ambient oxygen levels between the two regions, comparisons between Hawaiian and Californian animals are used to determine possible effects of oxygen

and food availability on metabolic rates. Buffering capacity was assayed to indicate an animal's capacity for anaerobic work (Castellini and Somero, 1981).

Materials and Methods

Cephalopods were captured on nine cruises aboard the R/V *Point Sur* and R/V *New Horizon* between September 1992 and September 1996. Sampling was done primarily in an area 160 km west of Point Conception, California (34° 37'N, 122° 42'W to 34° 30'N, 123° 20'W) and off Oahu, Hawaii (21° 20'N, 158° 20'W to 21° 35'N, 158° 35'W). Animals were collected using an opening/closing Mother Tucker trawl with a 10-m^2 mouth. The net was equipped with a 30-l thermally protecting cod end that reduced mechanical damage and heat shock to animals during recovery (Childress *et al.*, 1978). Ship speed was kept very low (0.5–1 kn) to decrease turbulence and abrasion in the net and to reduce the number of animals collected in the cod end. Upon reaching the surface, specimens were immediately transferred to 5°C seawater and allowed to recover for several hours. Only animals in the best physical condition were selected for physiological study. Animals were identified to species with the aid of several sources (Roper *et al.*, 1984; Sweeney *et al.*, 1992; Young, 1972; Hochberg, pers. comm.; Young, pers. comm.). Voucher specimens were preserved for verification of identifications.

Routine oxygen consumption rates were determined on board ship by allowing individual specimens to deplete the available oxygen in a sealed, water-jacketed chamber filled with filtered seawater containing 50 mg l^{-1} streptomycin (Childress, 1971a). All experiments were carried out at atmospheric pressure because hydrostatic pressure has been shown to have negligible effects on the metabolism of a mesopelagic squid, *Histioteuthis heteropsis* (Belman, 1978), and on several meso- and bathypelagic gelatinous zooplankters (Childress and Thuesen, 1993). Chambers were kept in darkness and, in most cases, the temperature was maintained at 5°C by means of a refrigerated water bath. Rates for individuals of some species were measured at either 2°, 3.5°, 10°, or 15°C and corrected to 5°C either using measured Q_{10} values or according to the methods outlined in Childress *et al.* (1990). The rate of change of the oxygen partial pressure within the respirometer was monitored using a Clark-type oxygen electrode (Mickel *et al.*, 1983) calibrated to air- and nitrogen-saturated seawater before and after each experiment. A magnetic stir pump mixed the water in the respirometry chamber and maintained water flow past the electrode without damage to the animals. Individual respiration experiments lasted from 2 to 24 h. Oxygen concentrations were averaged over 2-min intervals and recorded using a computer-based data

acquisition system. The mean rates of oxygen consumption between partial pressures of 30 and 70 mm Hg were used for comparisons because this allowed a period for the animals to calm down after being introduced to the chamber and ended before oxygen concentrations became limiting. Oxygen consumption rates of the smallest specimens were measured using glass syringes (3–50 ml) as miniature respiration chambers (Thuesen and Childress, 1993a, b) maintained in darkened water baths. Water samples were withdrawn periodically from the incubation syringe through a three-way valve using a gastight syringe, and the new incubation volume was noted. The oxygen content of the water sample was then analyzed using a gas chromatograph.

Oxygen consumption was calculated as micromoles of oxygen consumed per gram wet weight per hour. At sea, immediately following respiration experiments, animals were weighed using a motion-compensated shipboard precision balance system (Childress and Mickel, 1980). For additional comparisons, wet-weight-specific rates of oxygen consumption were corrected by covariance to 10 g by using measured scaling coefficients or an assumed scaling coefficient of -0.20 (Childress et al., 1990). The value of 10 g was chosen because it was the approximate modal weight of the animals measured. Both corrected and unscaled values for mean rates of oxygen consumption are presented in Table 1.

Mean rates of oxygen consumption were regressed against habitat depth. Because animals live at a range of depths, minimum depth of occurrence (MDO) was taken as the primary description of habitat depth. MDO is defined as that depth below which 90% of the individuals of a given species are captured in a given region (Childress, 1975). Ten meters was taken as the MDO for animals living at that depth or shallower to avoid distortions in regressions of ln-transformed data. MDO refers to the adult distribution except for species of the genus *Leachia*, as discussed later. For consistency with previous studies, animals that undergo a strong diel vertical migration are considered at their shallowest depth whether day or night. For comparison, regressions against minimum depth of daytime occurrence (MDdO) are also plotted. Both MDO and MDdO are listed in Table I. Estimates of cephalopod depth were based on collections from a variety of studies as well as on personal observations and communications (Pickford, 1946; Roper and Young, 1975; Young, 1978; Lu and Roper, 1979; Roper et al., 1984; Sweeney et al., 1992; James Hunt, MBARI, pers. comm.).

Regulation of oxygen consumption was measured by plotting specific rates of oxygen consumption *versus* partial pressures of oxygen. The critical partial pressure (P_c) was taken as the point at which oxygen consumption was no longer maintained independent of oxygen concentra-

tion. The P_c was determined by calculating regression lines for the two distinct parts of the relationship between oxygen consumption and P_{O_2}, the regulated (higher P_{O_2}) segment and the highly sloped (low P_{O_2}) segment. The P_c was designated as the intersection of these two lines.

In vitro buffering capacity (β) of mantle muscle, due to non-bicarbonate buffering compounds, was assayed following the methods of Castellini and Somero (1981). β is defined as the micromoles of base needed to change the pH of the homogenate by 1 pH unit per gram wet weight of muscle tissue. A unit of β is termed a "slyke." Although many cephalopod species use fins for sustained aerobic swimming, most cephalopods rely on mantle musculature for jet propulsion during burst escape responses (Baldwin, 1982). For this reason, and because it usually represents the largest percentage of body mass, mantle tissue was chosen for measurements of buffering capacity. Muscle tissue was homogenized at a dilution of 1:20 (weight:volume) in normal saline (0.9% NaCl). Homogenates were equilibrated to 20°C and stirred continuously during experiments. Homogenates were titrated from pH 6 to 7 using 0.2 N NaOH (less concentrated NaOH was used for animals with extremely low buffering capacities to get a sufficient number of points in the titration curve). If the homogenate had an initial pH greater than 6.0, it was acidified by the addition of HCl before the titration. As observed by Castellini and Somero (1981), more weakly buffered muscles yielded curves that tailed upward at pH values near 7.0 and above. In these cases, the linear portion of the curve (usually between pH 6.0 and 6.5) was used for calculating β. An Orion digital research ionalyzer (model 701A) was used with a glass pH electrode for monitoring pH changes. A microburet was used to add the NaOH solution.

All data analyses were performed with Statview II or SuperANOVA statistics programs (Abacus Concepts, Inc., Berkeley, CA). Simple linear regressions, *t* tests, and analysis of covariance (ANCOVA) were used. Mean values given are followed by the standard error. All regressions were carried out on ln-transformed data to linearize the data and maintain consistency with previous studies. The figures, however, are semilog plots. Confidence intervals for regression exponents are at the 95% level, *P* values for regression coefficients are *F* tests. ANCOVA was used to test whether the slopes and elevations of the various relationships were significantly different from zero and from each other. Regression slopes were declared significant when their slopes differed from zero at the 5% confidence level.

Results

The metabolic rates of 33 species of pelagic cephalopods from four orders are presented in Table I. An indi-
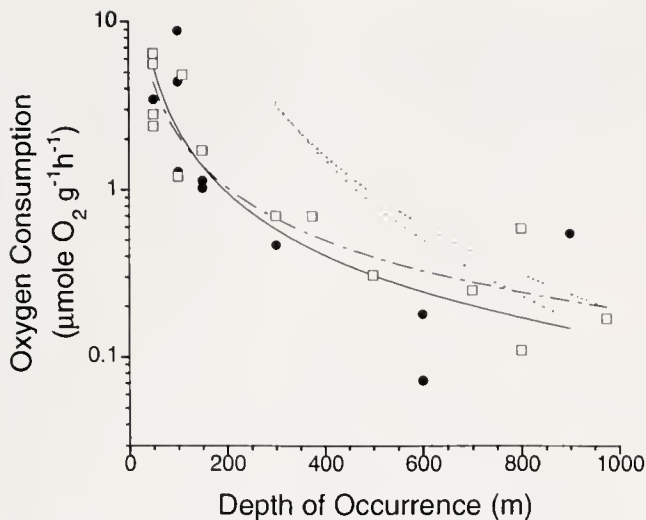
Figure 1. Mean oxygen consumption rates ($y = \mu\mathrm{mol}\ O_2\ g^{-1}\ h^{-1}$) of 23 species of pelagic cephalopods as a function of minimum depth of occurrence (x = meters). There is a significant decline in metabolism with minimum depth of occurrence for California (●) species ($y = 707.7x^{-1.25 \pm 0.58}$, $P = 0.001$; $R^2 = 0.68$) and Hawaiian (□) species ($y = 264.0x^{-1.05 \pm 0.55}$; $P = 0.001$; $R^2 = 0.87$). There is also a significant decline in metabolism with minimum depth of daytime occurrence for both Californian (· · ·) species ($y = 1.54*10^8x^{-3.07 \pm 2.33}$; $P = 0.01$; $R^2 = 0.43$) and Hawaiian (····) species ($y = 1.12*10^8x^{-2.24 \pm 1.65}$; $P = 0.002$; $R^2 = 0.62$). Results of ANCOVA show that there is not a significant difference in the slopes or magnitudes of the regressions of Californian and Hawaiian animals at either MDO or MDdO ($P > 0.4$).

vidual of *Vampyroteuthis infernalis*, which lives within the oxygen minimum layer between 600 and 800 m, had the lowest mass-specific metabolic rate ever measured for a cephalopod (0.02 μmol O_2 g^{-1} h^{-1}, 1050 g wet weight). *V. infernalis* had the lowest mean rate as well (0.07 ± 0.03 μmol O_2 g^{-1} h^{-1}; n = 15, 223.4 g mean wet weight). *Gonatus onyx*, a shallow-living vertical migrator, had a mean metabolic rate of 8.79 μmol O_2 g^{-1} h^{-1}, the highest rate measured in this study. Rates corrected to 10 g of wet weight ranged from 0.06 μmol O_2 g^{-1} h^{-1} for *V. infernalis* measured off Hawaii, to 6.55 μmol O_2 g^{-1} h^{-1} for *Gonatus onyx*. The mean rate presented here for *Histioteuthis heteropsis*, 1.02 ± 0.15 μmol O_2 g^{-1} h^{-1} (0.87 μmol O_2, corrected to 4.25 g for comparison with published values), is comparable to the value of 0.83 μmol O_2 g^{-1} h^{-1}, 4.25 g mean wet weight (Belman, 1978), the only other measurement of this kind available for a midwater cephalopod. Most physiological studies of cephalopods have been done on fast-swimming epipelagic squids that are capable of avoiding midwater trawls. DeMont and O'Dor (1984) reported a metabolic rate of 14 μmol O_2 g^{-1} h^{-1} for *Illex illecebrosus* at rest and 56 μmol O_2 g^{-1} h^{-1} at 100% activity (100-g animal, 13°C measurement temperature). These rates are similar to those observed for *Loligo forbesi* by Boucher-Rodoni and Mangold (1989).

Even with the exclusion of the faster epipelagic squids, a significant decline in mean metabolic rate (y) with MDO (x) was observed for both Californian and Hawaiian pelagic cephalopods (Fig. 1). There was no significant difference in either the slope (ANCOVA; $P = 0.47$) or the elevation (ANCOVA; $P = 0.98$) of the regression lines between Californian ($y = 707.7x^{-1.25 \pm 0.58}$; $P = 0.001$; $R^2 = 0.68$) and Hawaiian ($y = 264.0x^{-1.05 \pm 0.55}$; $P = 0.001$; $R^2 = 0.87$) species. A significant decline in metabolic rate (y) with minimum depth of daytime occurrence (MDdO) was also observed for both Californian and Hawaiian pelagic cephalopods (Fig. 1). Because of the absence of vertical migration among the deepest living species, estimates of daytime depth (x) result in a significantly steeper slope (ANCOVA; $P = 0.002$) for both Californian ($y = 1.54*10^8x^{-3.07 \pm 2.33}$; $P = 0.012$; $R^2 = 0.43$) and Hawaiian ($y = 1.12*10^8x^{-2.24 \pm 1.65}$; $P = 0.002$; $R^2 = 0.62$) regressions.

Normalization of metabolic rates to 10 g wet weight did not have a significant effect on the slopes or elevations of Hawaiian or Californian regressions against MDO or MDdO. The regression of cephalopod metabolism corrected to 10 g against MDO (Fig. 2) had a significantly steeper slope than the slopes for both fishes (ANCOVA; $P = 0.004$) and crustaceans (ANCOVA; $P = 0.001$) (data from Childress, 1975; Torres *et al.*, 1979). This relative steepness is driven both by higher metabolic rates among shallower animals (cephalopods living at 100 m have metabolic rates comparable to fishes and crustaceans living at the surface) and by lower metabolic rates among some deep-living cephalopods. It is interesting that the squids (order Teuthoidea) living below 300 m had significantly higher metabolic rates than other cephalopods (orders Octopoda and Vampyromorpha) (unpaired t test, $P = 0.0001$). The metabolic rates of teuthoids ($y = 117.9x^{-0.86 \pm 0.15}$; $P = 0.0001$; $R^2 = 0.66$) and octopods with *Vampyroteuthis infernalis* ($y = 16.8x^{-0.74 \pm 0.12}$; $P = 0.0007$; $R^2 = 0.87$) alone still decline with depth with a significantly steeper slope than either fishes or crustaceans.

Several specimens were excluded from the above analyses and are plotted separately (Fig. 3) because small numbers of captures and various life-history characteristics (*i.e.*, ontogenetic vertical migration, or pelagic stages of otherwise benthic animals) make depth distributions and metabolic data difficult to interpret. Inclusion of these species into the regression using roughly estimated MDOs does not significantly alter the slope or elevation of the regression of cephalopod metabolism with minimum depth of occurrence. *Ocythoe tuberculata* and *Amphitretus pelagicus* (both pelagic octopods), planktonic juveniles of the benthic octopus *Octopus rubescens*, and seven species of the family Cranchiidae (Teuthoidea) were among those excluded.

Table I

Metabolic rates and weight and depth data for 33 species of pelagic cephalopods from California and Hawaii

Species	Depth (m)* MDO	MDdO	n	T°C	Wet weight (g) Range	Mean	MO$_2$ (µmol O$_2$ g^{-1} wet wt h^{-1})† Range	Mean ± SE	Corrected
California									
Order Teuthoidea									
Gonatus onyx	100	400	1	5	—	2.30	—	8.79	6.55
Gonatus pyros	100	400	5	5	2.17–31.28	8.58	3.15–7.60	4.38 ± 0.84	3.41
Abraliopsis felis	50	300	1	5	—	0.99	—	3.44	2.16
			1	10	—	0.36	—	6.70	
Octopoteuthis deletron	100	300	1	5	—	8.19	—	1.28	1.22
Histioteuthis heteropsis	150	500	17	5	0.23–36.98	9.99	0.45–2.98	1.02 ± 0.15	0.73
			3	10	0.23–2.85	1.38	1.32–2.5	1.74 ± 0.38	
Histioteuthis hoylei	150	500	1	5	—	8.51	—	1.13	1.09
Chiroteuthis calyx	300	500	11	5	5.87–89.02	38.88	0.15–0.85	0.47 ± 0.07	0.67
Valbyteuthis oligobessa	900	900	1	2	—	25.40	—	0.55	0.66
Family Cranchiidae									
Galiteuthis phyllura	300	500	1	5	—	5.19	—	0.61	0.54
Cranchia scabra	10	10	1	5	—	35.39	—	0.29	0.37
Leachia dislocata	10	300	1	5	—	3.27	—	0.70	0.55
Helicocranchia pfefferi	300	300	6	5	0.15–3.60	0.88	0.41–1.94	0.97 ± 0.22	0.59
Order Octopoda									
Ocythoe tuberculata	10	10	1	5	—	1.21	—	4.17	2.73
Japetella heathi	600	600	11	5	0.84–162.5	35.19	0.03–0.28	0.18 ± 0.03	0.16
			1	10	—	6.32	—	0.48	
Octopus rubescens‡	10		2	5	0.04, 0.08	0.06	7.43–7.53	7.48 ± 0.05	2.78
			3	10	0.07–0.12	0.10	10.19–10.90	10.43 ± 0.23	
Order Vampyromorpha									
Vampyroteuthis infernalis	600	600	15	5	0.41–1050	223.4	0.025–0.41	0.07 ± 0.03	0.09
			1	10	—	4.74	—	0.31	
Hawaii									
Order Sepioidea									
Heteroteuthis hawaiiensis	110	250	1	5	—	5.88	—	4.81	4.31
Order Teuthoidea									
Abraliopsis pacificus	50	300	5	5	0.40–1.90	1.22	1.86–3.94	2.39 ± 0.39	1.63
			2	15	1.89–2.91	2.40	4.96–5.90	5.43	
Enoploteuthis higginsi	50	300	1	5	—	6.47	—	5.59	5.12
Pterygioteuthis microlampas	50	300	1	5	—	0.13	—	6.46	2.71
Octopoteuthis nielseni	100	300	1	2	—	0.13	—	1.20	0.61
Histioteuthis hoylei	150	500	2	5	0.40, 1.27	0.84	1.66–1.77	1.71	1.03
Chiroteuthis imperator	300	500	1	5	—	14.94	—	0.70	0.76
Joubiniteuthis portieri	500	500	3	5	36.00–48.99	41.85	0.20–0.39	0.31 ± 0.06	0.41
Mastigoteuthis famelica	375	675	1	5	—	4.06	—	0.70	0.59
Ctenopteryx siculus	50	625	1	5	—	4.24	—	2.81	2.37
			2	15	1.28, 2.11	1.70	5.07–5.41	5.24	
Bathyteuthis abyssicola	800	800	2	5	1.53, 37.7	19.6	0.56–0.61	0.59	0.59
Family Cranchiidae									
Leachia pacifica	50	50	3	3.5	0.90–2.12	1.52	0.24–1.83	0.81 ± 0.51	0.56
Liocranchia valdivia	500	500	12	5	0.17–21.28	2.92	0.27–1.61	0.56 ± 0.11	0.27
			11	15	0.02–19.0	2.25	1.47–3.47	2.47 ± 0.23	
Megalocranchia fisheri	10	600	1	5	—	47.9	—	0.39	0.54
Cranchia scabra	10	10	1	5	—	6.39	—	0.40	0.37
Order Octopoda									
Japetella diaphana	700	700	12	5	0.02–242	59.49	0.04–0.89	0.25 ± 0.07	0.15
			4	15	0.02–17.15	5.04	0.53–4.04	1.79 ± 0.82	0.52
Eledonella pygmaea	975	975	5	5	2.03–40.00	15.88	0.05–0.43	0.17 ± 0.07	0.18
			6	15	2.00–67.0	24.03	0.08–1.03	0.49 ± 0.11	
Amphitretus pelagicus	300	—	1	5	—	30.3	—	0.10	0.13
Order Vampyromorpha									
Vampyroteuthis infernalis	800	800	1		—	0.5	—	0.11	0.06

* MO$_2$: mean oxygen consumption rates measured from 70 to 30 mm Hg oxygen partial pressure. Values in the rightmost column are corrected to 10 g wet weight and 5°C (using scaling coefficients and Q_{10} values or assuming a scaling coefficient of −0.20 and a Q_{10} of 2.0).

†MDO: minimum depth of occurrence; MDdO: minimum depth of daytime occurrence.

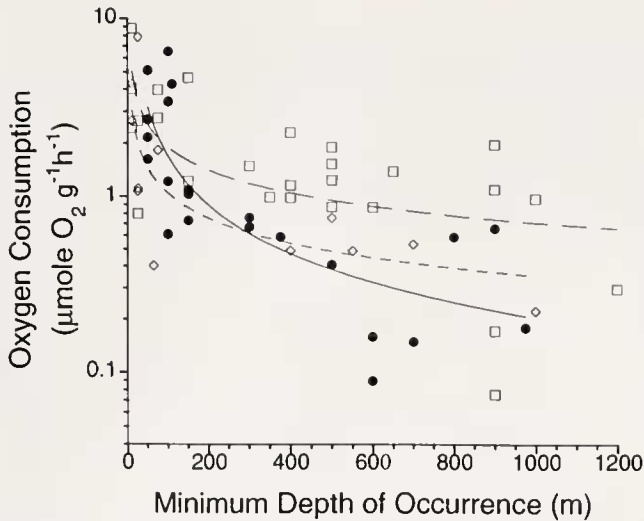‡The individuals of *Octopus rubescens* measured here are pelagic juveniles of an otherwise benthic species.

Figure 2. Oxygen consumption rates of cephalopods (●), fish ( ), and crustaceans (□) normalized to 10 g wet weight and 5°C as a function of minimum depth of occurrence. Results of ANCOVA show that the slope of the regression for cephalopods is significantly steeper than for either fish ($P = 0.004$) or crustaceans ($P = 0.001$) (data from Childress, 1973; Torres *et al.*, 1979).

The one specimen of *Ocythoe tuberculata* measured in this study was a male caught in an oblique tow from 2500 m to the surface. The animal's excellent physical condition upon reaching the surface suggests that it was caught at a shallow depth near the end of the trawl, but very little is known about its vertical distribution. It had

a metabolic rate of 4.17 μmol O$_2$ g^{-1} h^{-1}. The specimen of *Amphitretus pelagicus* measured was captured in a closing net at night between 700 and 820 m. There is some evidence that the juveniles of the species are found shallower than the adults, but adults have been captured as shallow as 250 m at night (Roper and Young, 1975). Nothing is known of its daytime distribution. Its metabolic rate (0.10 μmole O$_2$ g^{-1} h^{-1}) is very close to that of other deep-living pelagic octopods and to *Vampyroteuthis infernalis.*

Seven species of the family Cranchiidae were measured in this study. Limited data and questionable vertical distribution information failed to reveal a significant relationship with depth in these species. *Helicocranchia pfefferi* had the highest corrected (to 10 g wet weight) metabolic rate among the Cranchiidae (0.59 μmol O$_2$ g^{-1} h^{-1}, $n = 6$), but was not significantly different from other cranchiid species. Because many cranchiids undergo an ontogenetic migration (Young, 1975a, b), MDO was difficult to pinpoint. In the case of *Leachia pacifica* and *Leachia dislocata*, minimum depth refers to the larval habitat. Individuals of this species spend the majority of their lives in epipelagic waters and then migrate suddenly to great depths where maturation and spawning occur (Young, 1975a). The specimens of *L. pacifica* measured in this study were captured in shallow water, so its minimum depth is listed here as 50 m. Certainly for most of its life, *L. pacifica* is subject to the selection regime associated with epipelagic waters. *Galiteuthis phyllura*, *H. pfefferi*, and *Lio-*
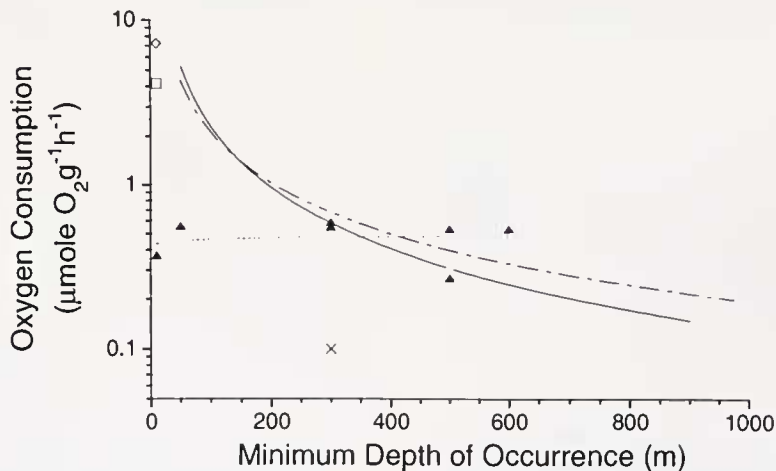

Figure 3. Mean oxygen consumption rates (μmol O$_2$ g^{-1} h^{-1}) normalized to a wet weight of 10 g (assuming a scaling coefficient of -0.20) of seven species from the family Cranchiidae (▲) as a function of habitat depth (m). The slope of the regression line is not significantly different from zero ($P = 0.57$). The regressions of Californian (——) and Hawaiian (—·—) cephalopods other than cranchiids are plotted as a function of minimum depth of occurrence for comparison (from Fig. 1). *Ocythoe tuberculata* (□) had an oxygen consumption rate of 4.17 μmol O$_2$ g^{-1} h^{-1}. Paralarval *Octopus rubescens* ( ) had a mean oxygen consumption rate of 7.27 μmol O$_2$ g^{-1} h^{-1}. *Amphitretus pelagicus* (×) had a metabolic rate of 0.10 μmol O$_2$ g^{-1} h^{-1}.

Table II

Critical oxygen partial pressures (P_c), weight-specific oxygen consumption rates (MO_2, μmol O_2 g^{-1} wet weight h^{-1}) as a function of body weight (M), and Q_{10} values for 10 pelagic cephalopods with different life-history characteristics

Species	P_c 5°C (mm Hg)	Wet weight (g) range	VO_2 = aM^b a;	VO_2 = aM^b b (±95% CI, n)	Mean MO_2 (±SE, n) 5°C	Mean MO_2 (±SE, n) 10°C	Mean MO_2 (±SE, n) 15°C	Q_{10}
California								
Order Teuthoidea								
Abrahopsis felis	—	0.36–0.99	ns	—	3.44 (—, 1)	6.70 (—, 1)	—	3.79
Histioteuthis heteropsis	6.97	0.23–36.98	1.16;	−0.20 (0.09, 17)	1.09*	1.74 (0.38, 3)	—	2.55
Order Octopoda								
Japetella heathi	6.10	0.84–162.5	ns		0.22 (—, 2)	0.48 (—, 1)	—	4.76
Octopus rubescens§	—	0.04–0.12	ns		7.48 (—, 2)	10.43 (0.23, 3)	—	1.94
Order Vampyromorpha								
Vampyroteuthis infernalis	3.10	0.41–1050	0.18;	−0.30 (0.10, 15)	0.11*	0.31 (—, 1)	—	7.90
Hawaii								
Order Teuthoidea								
Abrahopsis pacificus	—	0.40–2.91	ns		2.39 (0.39, 5)	—	5.43 (—, 2)	2.27
Ctenopteryx siculus	—	1.28–4.24	ns		2.81 (—, 1)	—	5.24 (—, 2)	1.86
Liocranchia valdivia	—	0.17–21.28	ns		0.56 (0.11, 12)	—	2.47 (0.23, 11)	4.41
		0.01–0.25†	ns		1.05 (—, 2)	—	2.56 (0.70, 3)	2.43
		0.37–21.3‡	ns		0.47 (0.08, 9)	—	2.43 (0.28, 8)	5.17
Bathyteuthis abyssicola	18.0	—	ns					
Order Octopoda								
Japetella diaphana	18.6	0.02–242	0.24;	−0.27 (0.05, 12)	0.44 (0.11, 6)	—	1.79 (0.82, 4)	4.10
		0.56–2.97†	ns		0.26 (0.01, 3)	—	0.60 (—, 1)	2.31
		17.0–36.0‡	ns		0.11 (—, 2)	—	0.53 (—, 1)	4.82
Eledonella pygmaea	—	2.03–40.0	ns		0.17 (0.07, 5)	—	0.57 (0.14, 5)	3.35

Critical partial pressure of oxygen (P_c) is defined as that partial pressure of oxygen at which oxygen consumption is no longer independent of oxygen concentration. All confidence intervals for scaling coefficients (b) are t tests at the 95% level of significance. Q_{10} values were calculated using rates from similar-sized animals.

* Rates corrected to appropriate weight for Q_{10} measurements using measured scaling coefficients.

† Weight range undergoing ontogenetic descent (captured between surface and 600 m depth).

‡ Adult weight range captured below 600 m depth.

§ Pelagic juveniles stage of an otherwise benthic species.

cranchia valdivia undergo a gradual ontogenetic descent. The specimens measured here were primarily small (10–30 mm mantle length) and are plotted at intermediate depths ranging from 300 to 500 m. *Cranchia scabra* has a very wide distribution. It has been captured from the surface to depths greater than 2000 m. It is plotted here at an MDO of 10 m.

Temperature effects

Metabolic rates were measured at 5°, and either 10° or 15°C for 10 cephalopod species with various life-history characteristics. Q_{10} values are presented in Table II. Q_{10} values were significantly lower for species that undergo diurnal vertical migrations through large temperature changes than for species with permanently deep (cold) habitats (unpaired t test, $P = 0.049$). The mean Q_{10} for vertical migrators was 2.62 ± 0.42 ($n = 4$), which is consistent with temperature responses observed previously

for vertically migrating crustaceans (Cowles *et al.*, 1991). The mean Q_{10} for non-migrators was 4.90 ± 0.78 ($n = 5$). Pelagic juveniles of *Octopus rubescens* were excluded from this comparison because nothing is known of their diel movements. The Q_{10} for *O. rubescens* was 1.94. Of the non-migrators, two species are known to undergo ontogenetic migrations from the surface to great depths. *Liocranchia valdivia* and *Japetella diaphana* both migrate from the surface as paralarvae to great depths as subadults. The Q_{10} values measured for individuals captured in the process of migration are similar to those of diurnally migrating cephalopods (2.31, 2.43), whereas the Q_{10} values for deep-living adults are considerably higher (4.82, 5.17). It should be pointed out that the non-migrators (including the adults of ontogenetically migrating species) live in water of about 5°C or below and rarely if ever encounter water as warm as 10°C. Their responses to temperatures of 10°C and above are thus not expected to be adaptive.
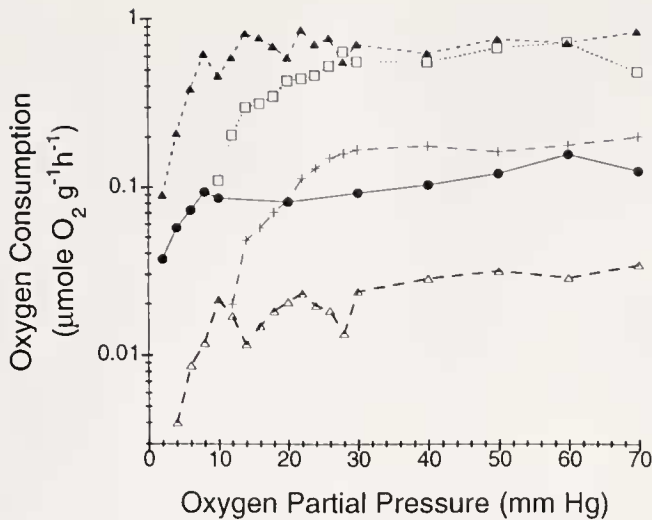
Figure 4. Mean oxygen consumption rates (μmol O$_2$ g^{-1} h^{-1}) averaged over 2-min intervals as a function of available oxygen (mm Hg) at 5°C. Individuals from five species are plotted. Mean critical partial pressures are 7.2 ± 1.4 mm Hg for *Vampyroteuthis infernalis* (△), 6.1 mm Hg for *Japetella heathi* (●), 21.8 ± 3.2 mm Hg for *Japetella diaphana* (+), 11.99 ± 2.28 mm Hg for *Histioteuthis heteropsis* (▲), and 18.0 for *Bathyteuthis abyssicola* (□).

Regulation

The regulation of oxygen consumption at 5°C was investigated in five species of pelagic cephalopods (Fig. 4). Critical partial pressures of oxygen (P_c) are presented in Table II. *Vampyroteuthis infernalis*, which lives permanently within the well-developed oxygen minimum layer off California, had a mean P_c of 7.2 ± 1.4 mm Hg ($n = 6$), which is comparable to that of the mysid *Gnathophausia ingens* (Childress, 1968; Sanders and Childress, 1990). One individual of *V. infernalis* demonstrated regulatory abilities down to 3.1 mm Hg, considerably lower than the minimum P_{O_2} of 6 mm Hg found within the California oxygen minimum layer. Similarly, *Japetella heathi*, a bathypelagic octopod found off the California coast, was capable of regulating its oxygen consumption to as low as 6.1 mm Hg ($n = 2$). *Japetella diaphana* off Hawaii, however, is apparently able to regulate its oxygen consumption to only 21.8 ± 3.2 mm Hg ($n = 3$), despite a metabolic rate very similar to that observed for *J. heathi* (Table 1). *Bathyteuthis abyssicola* from Hawaii regulated to 18 mm Hg ($n = 2$). The regulatory abilities of *J. diaphana* and *B. abyssicola* are consistent with the minimum value of 20 mm Hg found for the partial pressure of oxygen within the Hawaiian oxygen minimum layer. Regulatory abilities were assessed in four individuals of the vertically migrating squid *Histioteuthis heteropsis* captured off California. The mean critical partial pressure was 11.99 ± 2.28 mm Hg. One individual regulated

to 6.97 mm Hg, consistent with oxygen concentrations found at its deeper, daytime habitat.

Buffering capacity

The mean buffering capacities (β) in mantle muscle of eight species of pelagic cephalopods are listed in Table III. β ranged from 1.43 slykes for the Californian bathypelagic octopod *Japetella heathi* to 77.08 slykes for the epipelagic Hawaiian squid *Sthenoteuthis oualaniensis*. Significant scaling relationships could not be derived for any species measured. A significant decline in buffering capacity (y = slykes) with increasing MDO (x = meters) was observed ($y = 275.9x^{-0.67 \pm 0.39}$; $P = 0.004$; $R^2 = 0.85$; Fig. 5). The slope of this regression is significantly lower than the slope of the regression of oxygen consumption with depth (ANCOVA: $P = 0.009$).

Metabolic scaling

Regressions of weight-specific oxygen consumption against wet weight were significant in only three individual species (Fig. 6). *Vampyroteuthis infernalis* had a scaling coefficient, b, of -0.30 ± 0.10 ($P = 0.0001$; $R^2 = 0.75$), with weights ranging from 0.41 to 1050.0 g. *Histioteuthis heteropsis* had a scaling coefficient of -0.20 ± 0.09 ($P = 0.001$; $R^2 = 0.50$), with weights ranging from 0.23 to 36.98 g. The scaling coefficient found for *Japetella diaphana* was -0.27 ± 0.05 ($P = 0.0001$; $R^2 = 0.95$). Weights ranged from 0.02 to 242.17 g. The scaling coefficients for all three of these species are consistent with scaling data available for a wide range of animals (Schmidt-Nielsen, 1983). Sufficient range in size and numbers of *Chiroteuthis calyx* (5.97–89.02 g, $n = 11$) and *Japetella heathi* (0.84–162.5 g, $n = 11$) failed to yield a significant scaling relationship. Individuals of *J. heathi* larger than 10 g appear to follow a scaling pattern similar to that of *J. diaphana*, although the relationship was not significant.

There is a significant increase in wet weight (ln y = grams) with increasing MDO (ln x = meters) among the species for which oxygen consumption was measured ($y = 1.22x - 4.08$; $P = 0.0001$; $R^2 = 0.39$). The largest cephalopod measured in this study, an individual of *Vampyroteuthis infernalis* (1050 g), had the lowest metabolic rate measured (0.02 μmol O$_2$ g^{-1} h^{-1}). We were unable to measure oxygen consumption for the faster epipelagic squids, many of which reach sizes considerably larger than any species reported in the present study. Typical sizes of commercial species range from 0.1 to 1.0 kg (Roper *et al.*, 1984).

Discussion

A decline in metabolic rate with a species' minimum depth of occurrence (MDO) was observed for pelagic

Table III

Buffering capacity (β) of mantle muscle of pelagic cephalopods from California and Hawaii measured at 20°C;
wet weight and minimum depth of adult occurrence (MDO) are also given

Species	MDO (m)	n	Wet weight (g)		β	
			Range	Mean ± SE	Range	Mean ± SE
California						
Order Teuthoidea						
Gonatus onyx	100	1	—	1.06	—	32.61
Chiroteuthis calyx	300	5	3.43–70.08	36.96	7.43–9.86	8.37
Mastigoteuthis pyrodes	375	2	67.50, 96.98	82.25	8.00, 11.76	9.88
Cranchia scabra	10	2	16.14, 35.38	25.76	14.99, 30.77	22.88
Order Octopoda						
Japetella heathi	600	3	25.50–162.5	86.59	0.94–2.33	1.43 ± 0.45
Order Vampyromorpha						
Vampyroteuthis infernalis	600	13	5.93–600	224.35 ± 52.39	0.86–6.89	3.33 ± 0.45
Hawaii						
Order Teuthoidea						
Sthenoteuthis oualaniensis	10	1	—	110		77.08
Chiroteuthis imperator	300	3	27.7–53.56	40.07 ± 7.50	5.98–9.66	8.03 ± 1.08
Order Octopoda						
Japetella diaphana	700	7	8.96–325.8	119.10 ± 40.06	1.34–2.44	1.67 ± 0.15

cephalopods off California and Hawaii. This decline with increasing MDO is significantly steeper in slope than that observed for pelagic fishes and crustaceans (Fig. 2) (Childress, 1975; Torres *et al.*, 1979). The large decline results from both higher rates among shallower cephalopods and lower rates among many cephalopods living at depth. This means that many deep-living cephalopods have metabolic rates similar to those of midwater jellyfishes (Thuesen and Childress, 1994). The presence of

a strong decline in cephalopods, fishes, and crustaceans suggests, however, that the selective factors that influence metabolic parameters are similar at any given depth for all three groups. Buffering capacity has been used in the past to indicate the capacity of muscle tissue for anaerobic work (Castellini and Somero, 1981). Like oxygen consumption, β declined with increasing MDO. This is consistent with the results of Castellini and Somero (1981), who saw lower β values in deep-sea fishes than in either actively foraging pelagic ectotherms or in warm-bodied fishes.
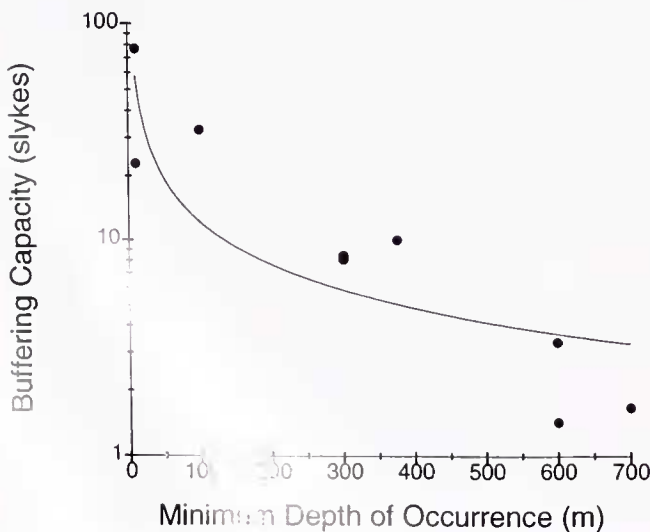
There are many variables confounded with habitat

Fig.   Buffering capacity (slykes) of mantle muscle as a function of minimum depth of occurrence in meters for nine cephalopods measured from California and Hawaii. The regression is $y = 275.9x^{-0.67 \pm 0.39}$ ($P = 0.004$; ... 85).
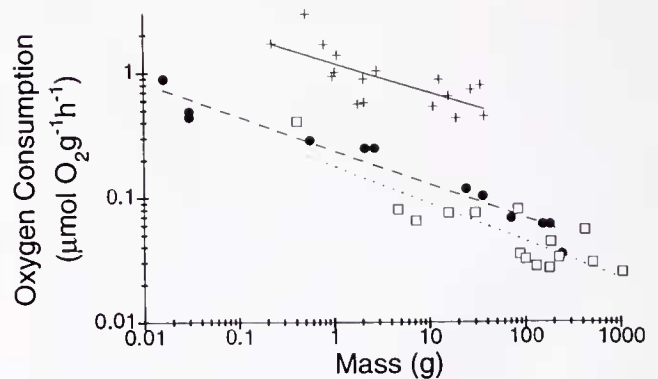

Figure 6. Oxygen consumption rates (μmol O_2 g^{-1} h^{-1}) as a function of wet weight (g). The slope of the regression line is $y = 1.16x^{-0.20 \pm 0.09}$ ($P = 0.001$; $R^2 = 0.50$) for *Histioteuthis heteropsis* (+), $y = 0.18x^{-0.30 \pm 0.10}$ ($P = 0.0001$; $R^2 = 0.75$) for *Vampyroteuthis infernalis* (□), and $y = 0.24x^{-0.27 \pm 0.05}$ ($P = 0.0001$; $R^2 = 0.95$) for *Japetella diaphana* (●).

depth. These include light, productivity, temperature, phylogeny, neutral buoyancy, vertical and horizontal migrations, oxygen concentration, and body size, among others. However, in the discussion below it will become apparent that the decline in metabolic parameters with increasing habitat depth most likely reflects decreased locomotory abilities in deeper-living animals. The steep slope of the regression of cephalopod metabolism with depth relative to that of fishes and crustaceans may reflect the relative efficiencies of locomotion at the surface, where high speeds are required for visually cued predator/prey interactions, and at depth, where sit-and-wait predation strategies are prevalent.

Light and visual interactions

According to the visual interactions hypothesis, reduced reliance on visual predator/prey interactions in the light-limited deep sea decreases selection for locomotory abilities, thus resulting in the lower metabolic rates observed in deep-living fishes, crustaceans, and cephalopods (Childress, 1995). This idea is supported by the presence of a decline in metabolism with depth among these visually orienting groups and the absence of such a decline among organisms that lack eyes (medusae and chaetognaths). That light-limited predator/prey interactions affect animal behavior is not a new idea. Light has long been recognized as a primary controlling factor in the daily movements of midwater organisms (Kerfoot, 1970). Limits on concealment from predation through counterillumination determine daytime depth distribution in some squids and fishes (Young *et al.*, 1980), and young cranchiid squids undergo ontogenetic changes that minimize their visibility at a given light level (Young, 1975b). These cranchiids can also control the orientation of their body and eyes to reduce the size of their own silhouette against surface illumination (Seapy and Young, 1986). The extent to which animals are concealed from visual predators and prey is suggested here to strongly influence the evolution of locomotory abilities and metabolic rates of midwater organisms. The metabolic rate of *Lolliguncula brevis*, which is typically found in complex and shallow coastal waters where opportunities for refuge and crypsis are greater, is half that of the more powerful squid living in open epipelagic waters. It was suggested that *L. brevis* is not required to swim great distances or at high speeds to capture prey or to escape predators (Finke *et al.*, 1996). The metabolic rates of fishes and crustaceans in benthic habitats, where opportunities for refuge and crypsis are greater, do not decline with increasing habitat depth to nearly the extent observed in pelagic animals (Childress *et al.*, 1990). The apparent lack of a decline in metabolic rates among cranchiid squids in the present study is probably a result of concealment from predation through transparency.

Productivity

The food limitation hypothesis suggests that animals living in relatively food-poor environments such as the deep sea have evolved lower metabolic rates as a way of conserving energy (Childress, 1971b; Smith and Hessler, 1974). If this were true, one might expect metabolic rates of deeper-living species to vary from region to region in correlation with surface primary productivity. Contrary to this prediction, comparisons between tropical and temperate regions of differing productivity have shown that among pelagic crustaceans living continuously below 400 m, there is no significant variation in metabolic rate with depth. In fact, shallow-living crustaceans actually have higher metabolic rates in Hawaii than in California where productivity is considerably higher (Cowles *et al.*, 1991). This may indicate an increased demand for strong locomotion for predator/prey interactions over greater distances in the clearer, more strongly illuminated surface waters. No significant differences were found between the slopes or magnitudes of the regressions of metabolism with depth for Californian and Hawaiian cephalopods. Although the magnitudes of the regressions were not significantly different, it may be worth noting that *Vampyroteuthis infernalis* seems (based on small numbers of captures) to come as much as 100 m shallower off California than off Hawaii. Similarly, *Japetella heathi* comes about 100 m shallower off California than does *J. diaphana* off Hawaii (Roper and Young, 1975; Young, 1978). This may reflect differing light regimes between the two regions.

Temperature effects

Temperature generally has large effects on metabolic processes. A 10°C increase in temperature typically causes a doubling of metabolic rate ($Q_{10} = 2$). Deep-living animals may be expected to have lower metabolic rates on the basis of lower temperatures alone. Donnelly and Torres (1988) report that the decline in aerobic metabolism of midwater fishes and crustaceans with depth in the eastern Gulf of Mexico is no greater than that due to the decrease in temperature. However, the observation that metabolism declines with increasing MDO in the isothermal waters of Antarctica (Torres and Somero, 1988; Ikeda, 1988) seems to eliminate temperature as the primary factor producing lower metabolic rates in the deep sea.

The Q_{10} values measured here (Table II) fall into two groups. Vertical migrators, which experience a wider range of temperatures every day, have typical responses to temperature, but non-migrators have much larger responses. Non-migrators typically live at or near 5°C and rarely, if ever, experience temperatures near 10°C. The responses to temperatures outside the normal range for the species are not expected to be adaptive. A few of the non-

migrators undergo ontogenetic descents through the water column. The young stages experience a wider range of temperatures over a relatively short (though unknown) period of time. Individuals captured during the process of ontogenetic descent have more typical responses to temperature than do the adults of the species. A Q_{10} of approximately 20 would be required to explain the slope of the decline in metabolic rates with depth observed here.

Phylogeny

Harvey and Pagel (1991) warned that interspecific comparisons may be invalid because phylogeny, instead of selection, may have played the greater role in determining the properties of the species. Although there are obvious phylogenetic effects, the observed variation with depth in the metabolism of cephalopods, like that of fishes and crustaceans, is probably not an artifact of phylogeny for two reasons (Childress, 1995). First, the physiological and morphological characteristics of related species seem to diverge as a function of habitat depth. Single genera or families of fishes and crustaceans often occupy the entire depth range studied, and the variation in a characteristic being studied may approach the entire range of variation for such a parameter within a data set (Childress *et al.*, 1990; Cowles *et al.*, 1991). Second, the evidence for convergent evolution among genera, families, and even phyla is strong. The origin of many of these groups lies outside the deep sea and thus can hardly produce a phylogenetic bias. Many deep-living groups share characteristics of chemical composition, general musculature, and physiology that all lead to decreased locomotory abilities. Cowles and Childress (1988) demonstrated directly that bathypelagic mysids have weaker swimming capabilities than do epipelagic species. Enzymatic activities provide evidence for reduced locomotory abilities in deeper-living fishes also (Childress and Somero, 1979; Sullivan and Somero, 1980).

Divergence of related species as a function of habitat depth can be seen at the ordinal level among cephalopods. Epipelagic squids (order Teuthoidea) are extremely active predators, and some are capable of speeds sufficient to propel their bodies out of the water (Cole and Gilbert, 1970). A study on *Illex illecebrosus* reported a respiration rate nearly twice as high as any cephalopod measured in this study (DeMont and O'Dor, 1984). Among the teuthoids measured here, nearly 2 orders of magnitude separate *Gonatus onyx*, a vertical migrator that lives below 100 m, and *Bathyteuthis abyssicola*, which lives continuously below 800 m. Similarly, *Octopus tuberculata* (order Octopoda), believed to be epipelagic, had a metabolic rate nearly 2 orders of magnitude higher than that measured for the pelagic octopods *Alloposus pelagicus* (captured at 700 m) and *Ja-*

petella diaphana (MDO = 700). Convergence of cephalopods with fishes and crustaceans living at similar depths is evidenced by both their morphology and metabolism. Voss (1967) recognized morphological similarities in cephalopods living at a given habitat depth. He observed a decrease in mantle musculature and the appearance of a gelatinous material that formed the bulk of the mantle in deep-living forms. In general, deeper-living cephalopods, like fishes and crustaceans, appeared to be relatively poor swimmers compared to their epipelagic counterparts.

Phylogeny does, however, appear to play at least some role in the evolution of cephalopod metabolism. Deep-living octopods have significantly lower metabolic rates than squids at similar depths. It appears from observations of the musculature (Roper, 1969), gill areas (Madan and Wells, 1996; Seibel and Childress, 1996), and metabolic rates that perhaps *Bathyteuthis abyssicola* leads a more active life than the deep-living octopods and *Vampyroteuthis infernalis*. However, the metabolic rate of *B. abyssicola* is still comparable to that of deep-living fishes with sit-and-wait predation strategies (Cowles and Childress, 1996).

The only family with representatives from a wide range of depths measured in this study is the Cranchiidae. Cranchiids comprise a monophyletic group distinguished from other cephalopods by many unique features (Nixon, 1983; Voss and Voss, 1983) that allow relatively low metabolic rates regardless of habitat depth. Foremost among these is the presence of a coelom, which provides neutral buoyancy (Denton and Gilpin-Brown, 1973; Clarke *et al.*, 1979) and may be contracted to create a flow of water over the gills. The mantle musculature is rarely used and then only for escape responses (Clarke, 1962). All cranchiids are largely transparent (Clarke, 1962; Seapy and Young, 1986), which decreases the selection associated with higher predation risks in higher levels of ambient light (McFall-Ngai, 1990). When disturbed, *Cranchia scabra* is also capable of filling its mantle cavity with seawater, which effectively doubles its volume (shipboard observations). It apparently shares this ability with at least one other cranchiid (Nixon, 1983). This sort of defense mechanism may reduce the need for lengthy escape swimming, and further emphasizes the trend among cranchiids to reduce metabolic costs. The limited data on metabolic rate and vertical distribution suggest that metabolism may be independent of habitat depth within this family (Fig. 3). Inclusion of the cranchiids does not significantly alter the slope or elevation of the regression in Figure 1.

Buoyancy

Many midwater cephalopods possess some means of achieving neutral buoyancy (Denton and Gilpin-Brown,

1973; Clarke, 1988; Clarke *et al.,* 1979; Voight *et al.,* 1994), whereas most epipelagic squids are negatively buoyant and rely on constant swimming for lift. It is conceivable that the metabolic rates of midwater cephalopods might be reduced simply by achieving neutral buoyancy, and that the higher metabolic rates of epipelagic cephalopods result from the added cost of support in the water column. Childress and Nygaard (1974) found, however, that neutral buoyancy in crustaceans does not appear to be a means of conserving energy *per se.* Metabolic rates were not correlated with density at a given depth. In epipelagic waters, locomotion is apparently a greater priority and dictates a high content of protein. Protein, associated with locomotory muscles, provides the density responsible for the negative buoyancy in such epipelagic squids as *Loligo* sp. and *Ommastrephes* sp. (Denton and Gilpin-Brown, 1973). Buoyancy can actually have a detrimental effect on locomotory abilities. Buoyancy organs make animals bulkier, which increases the energy needed for swimming at a given speed (Alexander, 1990; O'Dor and Webber, 1991). Although metabolism and buoyancy are certainly confounding factors, evidence suggests that the need for strong swimming determines the practicality of buoyancy. The energy required for support in the water column may be insignificant compared to an animal's overall activity level (Childress and Nygaard, 1974). However, when locomotion is not a high priority and activity levels are relatively low, the cost of support in the water column may be large relative to that of overall activity. In such situations, neutral buoyancy may be a cost-effective option. Among neutrally buoyant cephalopods there is still a decline in metabolic rates with increasing habitat depth.

Vertical migration

Many organisms undergo daily vertical migrations, spending the daylight hours at greater depths. Because vertical migrators are never exposed to surface daylight conditions, one might expect that light limitation on predator/prey interactions would result in metabolic rates more similar to those of deeper-living non-migrators than of epipelagic non-migrators. In previous studies (Childress and Nygaard, 1974), vertical migrators were considered at their shallowest depth (MDO) because it was the location of their primary food source. Evidence suggests that vertically migrating fishes and crustaceans are more similar in composition to shallow-living than to deep-living non-migrators (Childress and Nygaard, 1974). It was suggested that vertical migrators are essentially epipelagic animals that take refuge during the day at depth. However, *Gonatus* sp. and *Histioteuthis* sp., both vertically migrating cephalopods, have energy contents lower than those of epipelagic squids (Clarke *et*

al., 1985). The lower wet-weight-specific energy contents in some species are believed to be a result of increased water content, suggesting decreased locomotory abilities in those species. As discussed previously, Voss (1967) characterized organisms from various depths on the basis of morphological features such as body musculature, size and shape of fins and mantle, eye size, and skin color. He considered *Histioteuthis* to be a resident of the bathypelagic zone (700–2000 m) along with *Bathyteuthis.* By his criteria, *Gonatus* would have been placed in the mesopelagic zone (200–700 m), at a depth consistent with its deeper daytime habitat. The vast majority of epipelagic cephalopods exhibit some diel movements. Loliginids and ommastrephids (among others) migrate away from the surface during the day. A full moon, the equivalent of daylight at 300 m depth, has been shown to keep some ommastrephids away from the surface at night (Wormuth, 1976). This suggests that vertically migrating cephalopods may be following an isolume to which their metabolic rate may be adapted. The day and night habitats of vertical migrators are distinctly different, and both presumably have strong effects on the physiology of vertically migrating organisms. Both MDO and MDdO reveal a strong decline in cephalopod metabolism with increasing habitat depth (Fig. 1).

Horizontal migration

In addition to migrating vertically, many epipelagic squids migrate long distances horizontally. O'Dor (1992) has suggested that powerful squids have evolved to take advantage of current systems, and that this requires strong swimming and perhaps high metabolic rates as well. The deep sea has relatively weak currents, which may relieve animals from the selective pressures associated with current systems. However, this hypothesis probably applies only to truly large and active predators, all of which are capable of avoiding midwater trawls. Although nothing is known of the horizontal migration patterns of midwater cephalopods, none of the species studied here appear to be powerful swimmers of the caliber discussed by O'Dor (1992). Selection due to strong currents also cannot explain the lack of a decline in metabolism with depth in some phyla (cnidarians and chaetognaths; Thuesen and Childress, 1993a; 1994); patterns of vertical migration through varying current strengths; or differences in metabolic rates observed between Hawaii and California for shallow-water crustaceans (Cowles *et al.,* 1991).

Oxygen minimum layer

Another factor possibly selecting for lower metabolic rates at depth is oxygen concentration. Layers of low oxygen are found throughout the worlds' oceans at depths

between 200 and 1000 m. The oxygen minimum layer off California is particularly well developed. Partial pressures of oxygen reach a minimum of about 6 mm Hg between 600 and 800 m. Fischer and Bottjer (1995) suggest that the oxygen minimum layer provides refuge from large predators and that low oxygen has enforced passivity in animals that live within it. Certainly some larger predators are excluded from hypoxic waters (Carey and Robison, 1980). Reduced predation pressure may allow passive lifestyles. *Vampyroteuthis infernalis* is "oligoaerobic"—found only in low oxygen, with a peak concentration in the oxygen minimum layer (Pickford, 1946, 1952)—and had a metabolic rate of 0.09 μmol O_2 g^{-1} h^{-1}. Species of the genus *Japetella* also live within the oxygen minimum layer off both California and Hawaii and are relatively inactive metabolically. However, the mean metabolic rate of *J. diaphana* off Hawaii, where the oxygen seldom drops below 20 mm Hg, is not significantly higher than that of *J. heathi* off California. Fishes and crustaceans living below the oxygen minimum layer have been shown to have lower metabolic rates than others living directly within (Childress, 1995). This suggests that the low metabolic rates are not a specific adaptation to low oxygen and that passive lifestyles are selected for at great depths regardless of oxygen content.

Some animals possess specific adaptations to the oxygen minimum layer. *Gnathophausia ingens*, a deep-living mysid, has been shown to live aerobically within the minimum layer by being especially effective at extracting oxygen from the water. Its ability to regulate oxygen consumption to Po_2 values as low as 3 mm Hg is due in part to its ability to maintain a high ventilatory flow and to remove up to 50%–80% of the oxygen from the inhaled water (Childress, 1968, 1971a; Belman and Childress, 1976). The latter ability appears to stem from a hemocyanin with an unusually high affinity for oxygen and cooperativity of oxygen binding (Sanders and Childress, 1990). Regulation of oxygen consumption was measured in *Japetella diaphana, J. heathi, Histioteuthis heteropsis,* and *Vampyroteuthis infernalis.* Like *G. ingens,* both *J. heathi* and *V. infernalis* off California can regulate oxygen consumption to at least 6 mm Hg, allowing aerobic living even at the lowest environmental oxygen levels found there. Two individuals of *V. infernalis* regulated successfully below 4 mm Hg. *J. diaphana,* however, regulated oxygen consumption to a mean of 21.8 mm Hg, which corresponds to the minimum environmental Po_2 value of 20 mm Hg off Hawaii. *Histioteuthis heteropsis,* which migrates into the oxygen minimum layer during the day, was previously reported by Belman (1978) to be incapable of regulating to oxygen concentrations required for aerobic living within the minimum layer (P_c = 20.0 mm Hg). In contrast to those earlier studies, in

our studies *H. heteropsis* was able to regulate its oxygen consumption to at least 7 mm Hg. The mean critical partial pressure for this species was 11.99 $\pm$ 2.28 mm Hg. The lowered metabolism at low temperatures may allow aerobic living for some animals, such as *H. heteropsis,* migrating into the cooler waters of the oxygen minimum layer during the day. Cowles *et al.* (1991) found a strong effect of temperature on the critical oxygen partial pressures of vertically migrating crustaceans. This is consistent with findings by Sanders and Childress (1990) that the oxygen affinity of hemocyanin from several of these species is temperature-dependent and increases greatly at low temperatures.

Oxygen extraction and jet propulsion are incompatible functions in cephalopods (Wells, 1988). To maximize oxygen extraction, water must be passed relatively slowly over the gills and out the jet. Maximization of propulsion requires the ejection of water at a velocity sufficient to generate the required thrust. *Nautilus pompilius,* for example, can extract 20% of the available oxygen from the ventilatory stream at rest, but only 5% or less during active propulsion (Wells and O'Dor, 1991). Epipelagic squids have maximized locomotion and are able to extract oxygen at levels necessary to fuel high speeds only because water flow over the gills increases as swimming speed increases. Circulatory adaptations, including enhanced unloading of oxygen at the tissues and a large positive Bohr shift, allow efficient use of nearly all of the oxygen taken up by the blood (Zammit, 1978). Benthic octopods, on the other hand, have optimized oxygen extraction. The respiratory pigments of octopods have a greater affinity for oxygen than do pigments in the faster squid and sepioid species (Brix *et al.,* 1989). In addition, their slow benthic lifestyle allows a reduction in mantle contractions and a slow flow of water over the gills. The decreased reliance of deep-living cephalopods on locomotory abilities, implied by the decline in metabolism with depth, would, as in benthic octopods, allow a slowing of the ventilatory stream and more efficient extraction of oxygen—adaptations compatible with life in a reduced oxygen environment.

Buffering capacity

Reduced buffering capacities in mantle muscle at depth are further evidence that locomotory abilities are not strongly selected for in the deep sea. A high buffering capacity allows prolonged glycolytic work such as that required for extended burst escape responses. The sit-and-wait predation strategies prevalent through much of the deep sea do not require a high capacity for anaerobic work. Differences in oxygen levels between California and Hawaii might be expected to yield higher short-term anaerobic capacities in animals that live in the lower ox-

ygen habitat. A lesser oxygen supply would more quickly lead to functional anoxia (tissue energy demand outstrips aerobic capacity). However, no difference in β was seen between *Japetella diaphana* and *J. heathi*. Both species, like *Gnathophausia ingens*, appear to have very limited anaerobic abilities. Buffering capacity is believed to be an adaptable parameter that can be altered to match metabolic function (Castellini and Somero, 1981) and has been correlated with tissue capacity for glycolytic energy production in response to functional anoxia (Eberlee and Storey, 1984). The fact that no difference was seen between similar animals in different oxygen environments is evidence that the reduced locomotory abilities are not a response to ambient oxygen levels.

Metabolic scaling

The body size of the pelagic cephalopods measured in this study increased with increasing MDO (largely because the large epipelagic species were not sampled). Because mass-specific metabolism has, with notable exceptions (DeMont and O'Dor, 1984; Thuesen and Childress, 1994), been repeatedly shown to decrease with increasing body mass (Schmidt-Nielsen, 1983), body size could have significant effects on metabolic estimates based on depth of occurrence. Scaling coefficients could be derived for only three species: *Vampyroteuthis infernalis, Japetella diaphana*, and *Histioteuthis heteropsis*. Scaling coefficients for all three ($b = -0.30, -0.27$, and -0.20 respectively) fall within the range of most animals (Schmidt-Nielsen, 1983). Sufficient range in size and numbers failed to yield a significant scaling relationship for *Chiroteuthis calyx*. This is perhaps due to the drastic change in body proportion from the "doratopsis" paralarval stage, a characteristic of this genus, to adulthood (Vecchione *et al.*, 1992). Significant scaling relationships could not be derived for the remaining species, owing either to lack of sufficient numbers of specimens or to insufficient size ranges. Normalizing metabolic rates to 10 g, either by assuming a scaling coefficient of -0.20 (Schmidt-Nielsen, 1983) or by using measured coefficients where possible, did not have a significant effect on the slopes of the regressions with depth. A scaling coefficient of approximately -1.8, based on the increase in body size with depth observed in this study, would be required in order for size to account for the observed variation with depth. A significant increase in body size with depth was observed among the animals for which β was assayed as well. However, no significant size-scaling was observed for buffering capacity.

Locomotory efficiency

Packard (1972) compared fish and cephalopod "modes of life" and distinguished these organisms from crustaceans and other molluscs in terms of their "great ability to travel." He observed that functionally, squid are fish. But many deep-living cephalopods actually have much lower metabolic rates than do fishes or crustaceans living at similar depths. The slope of the regression of 10-g-corrected oxygen consumption with MDO is steeper for cephalopods than for both fishes and crustaceans (Fig. 2). The metabolic rates of *Vampyroteuthis infernalis* and the deep-living pelagic octopods are more comparable to those of similar-sized scyphomedusae (Thuesen and Childress, 1994) than to those of fishes or crustaceans. Although the rates of deep-living squids are similar to those of fish with sit-and-wait predation strategies (Cowles and Childress, 1996), shallow squids have higher rates than do fish or crustaceans at similar depths. The slope of the regression of metabolism with depth is steeper for teuthoids and octopods, considered separately, than for fishes and crustaceans. More efficient locomotion among deeper-living cephalopods may be responsible for this difference. Shallow-living cephalopods rely extensively on jet propulsion to gain high speeds. Because the energy required for thrust increases with the velocity squared, high-speed jet propulsion is inherently inefficient (Vogel, 1994). Yet most shallow-living squids retain jet propulsion as the primary means of locomotion (Baldwin, 1982; Hoar *et al.*, 1994). Hoar *et al.* (1994) did note, though, that the slower coastal species such as the loliginids use their fins, which are large, more actively than do the oceanic ommastrephids, which use their smaller fins as rudders during extremely high-speed swimming.

Deep-living cirrate octopods have been observed using the arms and web to swim in a manner similar to the "bell-swimming" of medusae (Vecchione and Roper, 1991). *Cirrothauma murrayi* relies very heavily on fins for locomotion (Aldred *et al.*, 1983). It has also been seen using the arms and web as a "balloon" for defense, eliminating costly escape swimming (Boletzky *et al.*, 1992). *Vampyroteuthis infernalis, Chiroteuthis calyx*, and *Histioteuthis heteropsis*, among others, have been observed swimming primarily with fins (James Hunt, pers. comm.). Fin- and bell-swimming are cost efficient compared to jet propulsion by means of mantle contractions, due to reduced speeds (reduced drag) and to the large water masses (relative to body mass) being processed (Vogel, 1994). Although their morphology suggests that *Octopoteuthis* spp. (MDO = 100 m) rely heavily on fins for swimming, limited video footage shows *O. deletron* swimming with slow contractions of the mantle while holding the large fins curved over the body so that water passes beneath them (James Hunt, pers. comm.). The metabolic rates of *O. deletron* and of *O. nielseni* are low compared to those of other squids at similar depths. Perhaps the curious fin posture provides static lift that re-

duces the metabolic costs associated with support in the water column. This species also attains considerable size, which would deter predation (Roper et al., 1984). Again, among the cranchiids, where transparency has alleviated much of the need for high-speed swimming, mantle contractions are rarely used for locomotion (Clarke, 1962).

Morphology and limited shipboard observations indicate that some deep-living cephalopods do utilize jet propulsion as a primary means of locomotion. At extremely low speeds, jet propulsion may not be so costly, which might explain the existence of slow jetters such as jellyfish and salps (Vogel, 1994). It might also explain the extremely low metabolic rates of deep-living pelagic octopods. These organisms process large amounts of water through a relatively large funnel opening, resulting in efficient, low-speed swimming. It is also possible that they utilize the arms and web for bell-swimming, much as the cirrate octopods do. There is tremendous diversity in the swimming behaviors of pelagic cephalopods but, perhaps because high speeds are not a priority in the deep sea, a more efficient means of locomotion is desirable.

Despite differences in their locomotory efficiencies, buoyancy mechanisms, and structural compositions, fishes, crustaceans, and cephalopods show similar metabolic trends with depth; these trends probably reflect the presence of highly evolved eyes in these groups. The results presented here emphasize the importance of differential selection for locomotory abilities with habitat depth in determining the metabolic rates of organisms. Available evidence implicates vision as a selective factor strongly affecting the evolution of locomotory abilities. Although one may intuitively suspect food availability or low oxygen, the declines in both oxygen consumption rates and pH buffering capacity of locomotory muscles with depth in pelagic cephalopods point to a different conclusion. These factors support the hypothesis that the extent to which visual predator/prey interactions occur is largely responsible for the decline in metabolic rates of visually orienting, midwater organisms with increasing minimum depth of occurrence. Although cephalopods have often been compared with fishes in discussions of ecology and locomotion, we conclude that pelagic cephalopods living in the deep sea might be more appropriately compared with medusae in these contexts.

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